

THE CONTRIBUTION OF THE MICROFAUNA TO TOTAL SOIL METABOLISM

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It appears to me that, in our discussions at this meeting, we have to fulfil two distinct objectives. Firstly we must use this unique opportunity for students of two different aspects of soil science to compare their results and their objectives so that both facts and ideas can be compared in a different context. Secondly, because an experience such as this makes us think over our own reasons for undertaking particular lines of research, I, as an animal ecologist for instance, must state more explicitly to my zoologist colleagues what I am doing and why. These two themes can certainly be united, but in a short talk it is not easy to satisfy both groups of listeners. I must not puzzle the microbiologists with the private jargon of the zoologists nor should the latter be bored by repetition of familiar material. I am therefore going to talk about a rather simple theme, that of the role of the soil fauna in liberating energy and nutrients from dead plant matter, and to try to draw together the main results from a wide range of data, almost all of which are already published. I shall not take time here to re-argue the validity of metabolic measurements in the ecological field (MACFADYEN 1961, 1962).

If we construct a balance-sheet (MACFADYEN in press) for the total annual flow of energy through a meadow exploited by man by means of grazing cattle (Fig. 1), we find that, of the total energy captured by plant photosynthesis, less than one seventh is respired by the plants, about two sevenths are consumed by herbivores and four sevenths are not exploited until the plant tissue has died. This shows that even when man does his best to exploit herbage the biological properties of grass are such that it is only eaten to a small extent during life. A very much smaller extent, for instance, than in the case of phytoplankton. It follows that earlier ideas about the community consisting mainly of a trophic pyramid of herbivores feeding on plants and themselves forming the food of carnivores is an over-sim-

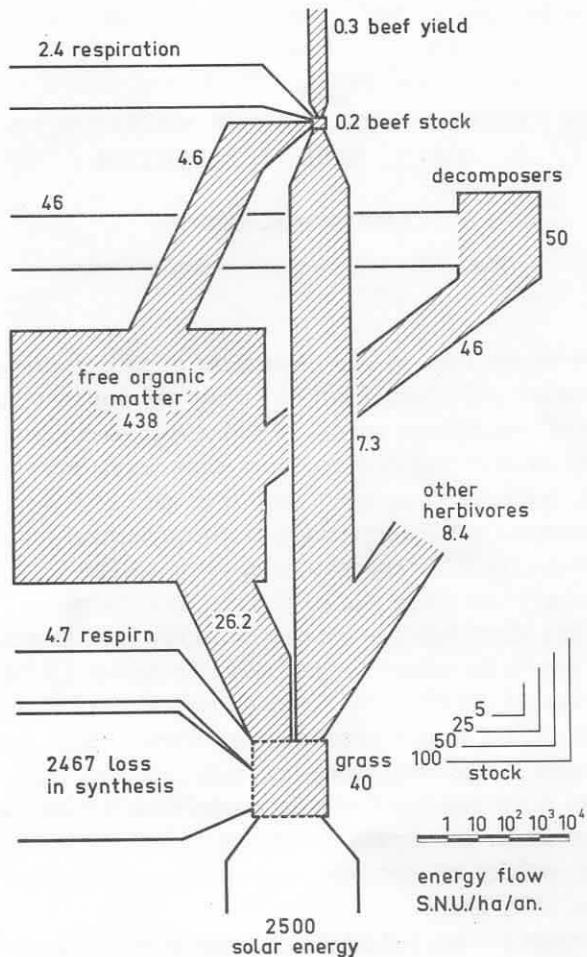


Fig. 1. Scale diagram of energy flow in a grazed meadow.

Shaded area is organic matter, unshaded is energy.

Areas of boxes are proportional to \log_{10} calorific content of stock in Standard Nutritional Units per Hectare (1 S.N.U./ha = 100 k-cal/m²). Widths of flow channels are proportional to \log_{10} energy flow in S.N.U./ha/annum.

plification because in the meadow this food chain attracts barely half as much of the energy flow as does the food web which contains the decomposer organisms.

If the dead plant matter were allowed to accumulate, the nutrients it contains would be prevented from returning to the plants and the com-

munity would become steadily less fertile as is well known to happen when, often through human mis-management raw humus formation occurs. Even in a meadow on a mull soil the fact that the ratio of the calorific content of the humic organic matter to the rate of energy flow is high indicates that the decomposers effectively hold up the oxidation of this matter and concomitant liberation of nutrients.

It is of interest therefore, to try to find out which workers in the decomposer "industry" are responsible for most of the breakdown by measuring the metabolism of the different species present in a wide range of soils. This is the approach which I and my colleagues are adopting, but it is a very slow business. To be done adequately we need to know how many animals of which species are present throughout the year, what the age composition of each species population is and how metabolic rate is related both to age and to soil climate conditions obtaining at the time of each census. Every stage of this programme is beset with technical difficulties, as you will realize, and I doubt if in my lifetime we shall gain such information for more than a few representative species in some selected habitats.

In the absence of such results we have to be satisfied with approximations, however crude, if we would try to obtain a wider view of the structure of the decomposer web in soils. From American work on simpler habitats, for example that of ODUM and SMALLEY (1959) on the invertebrates feeding on *Spartina* we learn that large seasonal changes in age composition and metabolic rate operate in opposite senses so that their product (which is population metabolic rate) is nearly constant throughout the period of available food. This kind of result, together with those I shall present below, lead one to hope that the overall picture may be less complex than its components. Here I propose to make use of published data to assess the range of results we may expect to obtain from soil.

In 1930, BORNEBUSCH published a remarkable pioneer book in which he attempted to do just this. Although some of his census figures in particular are much too low we can attempt to correct for imperfections in his technique and five of his forest soil types are included in the subsequent analysis. In addition, I have used VAN DER DRIFT's (1951) beech forest figures, two sets of CRAGG's (1961) high altitude moorland data suitably corrected for temperature and figures of OVERGAARD NIELSEN's (1949, 1961) on Enchytraeids and Nematodes. I have added the composite figures for grazed meadow (MACFADYEN, 1961, inpress) although it should be remembered that this represents a man managed system subject to added fertilizers.

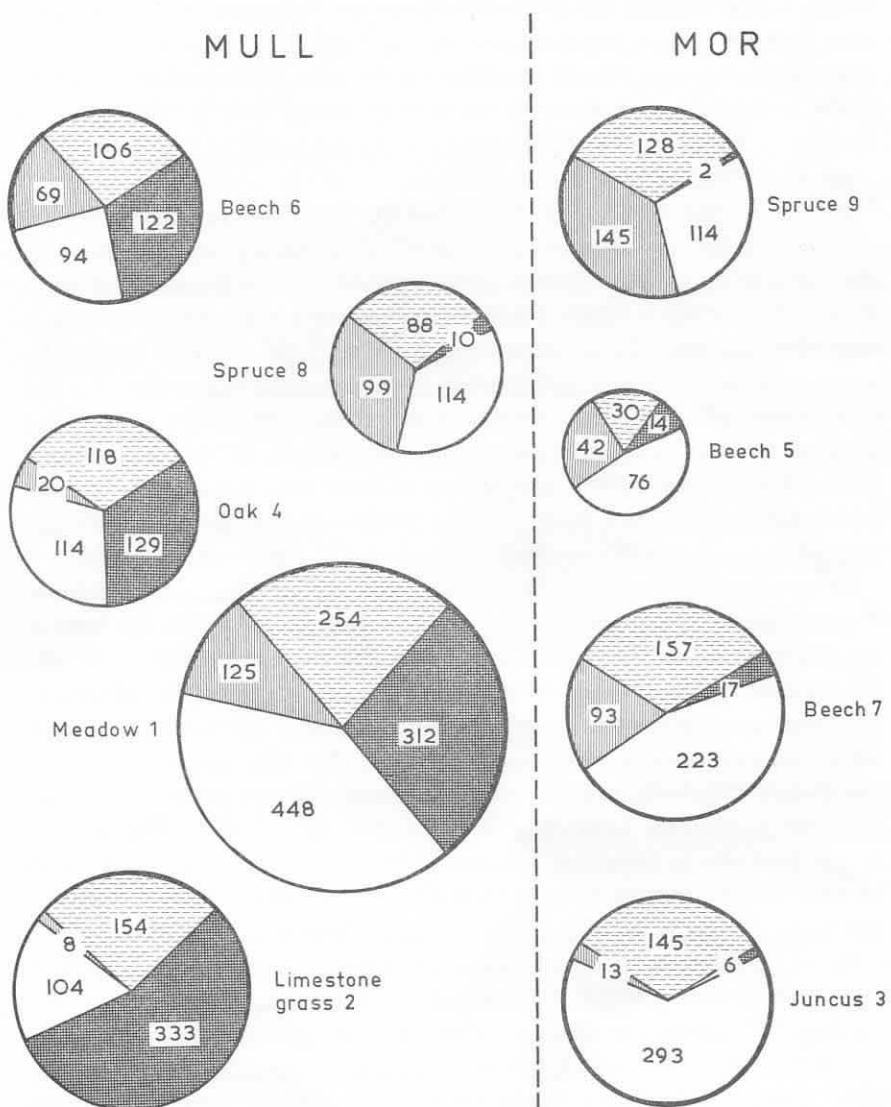


Fig. 2. Comparison of total annual respiration in nine soil types. 1. MACFADYEN (1961); 2 and 3 CRAGG (1961); 4, 6, 7, 8 and 9 BORNEBUSCH (1930), localities 10, 15, 4, 1 and 6; 5 VAN DER DRIFT (1951).

Sectors represent (clockwise from the top) herbivores, large decomposers, small decomposers, predators.

The fauna is split into four groups, herbivores, carnivores, large decomposers, those which have a mechanical effect on the soil, and small decomposers. Each of these categories is then subdivided into the major taxonomic constituents with some such as Nematodes, beetles and flies being appropriately divided between two groups. For each group I have estimated an annual metabolic rate following the principles pioneered by NIELSEN (1961). It is unnecessary to add that results of this kind are very approximate indeed.

In Table 1 the analysis of nine soil habitats by biomass and metabolism is given. In Fig. 2 the areas of the circles represent the total annual metabolism in kilocalories per square metre, the areas of the sectors being proportional to the rates for each of the trophic groups (herbivores are at the top, large and small decomposers and predators in clockwise succession). A comparison of the total areas reveals at once a rather striking similarity when it is remembered that the soil types covered include a moorland *Juncus* habitat, mull and mor forest and a rich pasture. The overall ratio in areas is seven to one and if the meadow is excluded for the reason already given it falls to only four to one.

When the sizes of the sectors are compared the following suggestions which may be established or disproved by further study, present themselves:

- 1) The poverty of large decomposers in mor soils seems to be reflected, in the small size of the second sector in such soils.
- 2) The tendency for small decomposers to compensate to a large extent for the absence of large decomposers in mor soils. This presumably corresponds to previous reports (NIELSEN, 1949) and with the fact that many mor soils differ from mulls mainly in the length of time that the litter remains on the soil surface, not in an actual accumulation of peat.
- 3) The rather constant proportion of herbivore metabolism in all the soil types.
- 4) The great variability in the proportion and magnitude of predator metabolism. The spruce and beech woods seem to have a high proportion of predators and one naturally speculates whether this is related to the continuous presence of cover and the favourable microclimate.

Generalizations of this kind are of little value without a sound taxonomic basis and I have included in table 1 and figures 3, 4 and 5 a further analysis of each trophic group in turn. The large decomposers behave much as one would expect, the earthworms dominating the mull soils but being partially replaced by Isopods and Myriapods in some cases. The outstanding feature of the remaining figures is that, despite a restricted range of total metabolism

TABLE 1. Analysis of nine soil habitats by biomass and metabolism

		1				2				3				4			
		cal/g/ day at 16°C	g/m ²	kcal/ m ² /ann.	% of group	Upland limestone grass	g/m ²	kcal/ m ² /ann.	% of group	Upland <i>Juncus</i> Moor	g/m ²	kcal/ m ² /ann.	% of group	Oak mull (10)	g/m ²	kcal/ m ² /ann.	% of group
Herbivores	Nematodes . .	144	6.0	183.2	72.1		0.5	4.8	3.0		1.1	13.7	9.5		2.0	61.1	51.6
	Molluscs . .	29	10.0	61.5	24.2										5.3	32.7	27.6
	Bugs	30	0.2	1.3	0.5												
	Lepidopt. et al	35	0.1	0.7	0.3										0.6	4.1	3.4
	Beetles	40	0.1	1.1	0.4										0.2	1.5	1.3
Large decomposers	Diptera	29	1.0	6.1	2.4		36.0	149.0	97.0		21.7	131.3	90.5		3.1	19.0	16.1
	Total		17.4	253.9			36.5	153.8			22.8	145.0			11.2	118.4	
	Lumbricids . .	7	120.0	178.1	57.2		137.0	333.0	100.0		1.0	5.5	100.0		61.0	90.5	70.4
	Isopods . . .	36	5.0	38.2	30.6										0.3	2.1	1.7
	Diplopods . .	36	12.5	95.4	12.3										4.7	35.9	27.9
Small decomposers	Total		137.5	311.7			137.0	333.0			1.0	5.5			66.0	128.5	
	Nematodes . .	144	6.0	183.2	40.9		0.4	4.8	4.6		0.5	6.8	2.3		1.0	30.5	26.6
	Enchytraeids .	40	12.0	102.0	22.8		15.0	76.0	73.0		53.0	269.0	91.7		0.7	5.8	5.0
	Oribatids . .	24	2.0	10.2	2.3		0.3	8.3	8.0		0.4	13.0	4.4		0.4	2.0	1.7
	Collembola . .	144	5.0	152.6	34.0		0.6	15.1	14.5		0.1	4.1	1.4		0.1	76.3	66.6
Predators	Total		25.0	448.0			16.3	104.2			54.0	292.9			1.8	114.6	
	Spiders	27	6.0	34.3	27.5										0.1	0.3	1.5
	Opiliones . .	53	0.4	4.5	3.6												
	Centipedes . .	60	1.0	12.7	10.2		1.3	8.3	100.0						0.6	7.8	34.9
	Parasitids . .	300	1.0	63.6	51.0						0.2	13.0	100.0		0.2	12.7	57.5
	Flies	30	0.2	1.3	1.0												
	Beetles	39	1.0	8.3	6.7										0.2	1.4	6.4
	Total		9.6	124.7			1.3	8.3			0.2	13.0			0.9	22.2	
	Grand total .		189.5	1139.3			191.1	599.5			78.0	456.4			79.9	383.7	

5			6			7			8			9		
Beech R.H.			Beech Mull (15)			Beech R.H. (4)			Spruce Mull (1)			Spruce R.H. (6)		
g/m ²	kcal/m ² /ann.	% of group	g/m ²	kcal/m ² /ann.	% of group	g/m ²	kcal/m ² /ann.	% of group	g/m ²	kcal/m ² /ann.	% of group	g/m ²	kcal/m ² /ann.	% of group
0.1	3.4	10.0	2.0	61.1	57.4	2.0	61.1	38.8	2.0	61.1	69.3	2.0	61.1	47.6
2.6	15.9	47.5	5.0	30.4	28.6	3.2	19.7	12.5	0.2	1.0	1.1	0.2	0.9	0.7
0.5	3.2	9.5												
0.1	0.7	2.0	0.6	4.2	3.9	0.5	3.9	2.5	1.3	9.6	10.8	1.1	8.3	6.5
0.8	6.7	20.1	0.2	1.5	1.4	3.5	29.5	18.7	0.9	7.5	8.5	3.7	31.5	24.5
0.6	3.7	11.0	1.5	9.3	8.7	7.0	43.3	27.5	1.5	9.2	10.4	4.3	26.5	20.6
4.7	33.6		9.3	106.5		16.2	157.5		5.9	88.4		11.3	128.3	
2.9	4.3	30.7	53.1	63.8	52.2	5.4	8.0	47.1	5.1	7.5	73.2	0.9	1.3	63.8
0.0	0.0		0.2	1.1	0.9	0.1	0.4	2.2	0.0	0.0		0.0	0.0	
1.3	9.6	69.3	7.5	57.2	46.9	1.1	8.6	50.6	0.4	2.8	26.8	0.1	0.8	36.2
4.2	13.9		60.8	122.1		6.6	17.0		5.5	10.3		1.0	2.1	
0.7	21.4	28.1	1.0	30.5	32.6	1.0	30.5	13.7	1.0	30.5	26.9	1.0	30.5	26.9
0.0	0.0		1.1	9.1	9.7	1.6	13.2	5.9	0.0	0.2	0.1	0.1	1.1	1.0
1.6	8.2	10.8	0.2	8.1	8.7	0.2	11.2	5.0	0.3	14.2	12.5	0.4	20.9	18.4
1.5	46.4	61.0	0.1	45.8	48.9	0.2	168.0	75.3	0.1	68.8	60.5	0.1	61.0	53.7
3.8	76.0		2.4	93.5		3.0	222.9		1.4	113.7		1.6	113.5	
0.5	2.8	6.7	0.0	0.2	0.2	0.1	0.7	0.8	0.0	0.2	0.2	0.0	0.2	0.2
0.0	0.2	0.5												
0.8	9.5	22.9	1.3	16.4	23.9	0.5	6.5	6.9	0.6	7.1	7.2	0.7	9.4	6.4
0.3	19.7	47.4	0.1	50.9	74.0	0.1	82.7	88.5	0.1	89.0	89.7	0.2	133.6	91.5
0.6	3.8	9.2												
0.7	5.5	13.3	0.1	1.2	1.7	0.4	3.6	3.8	0.4	3.0	3.0	0.3	2.7	1.8
2.9	41.5		1.5	68.7		1.1	93.5		1.1	99.3		1.2	145.9	
15.6	165.0		74.0	390.8		26.9	490.9		13.9	311.7		15.1	389.8	

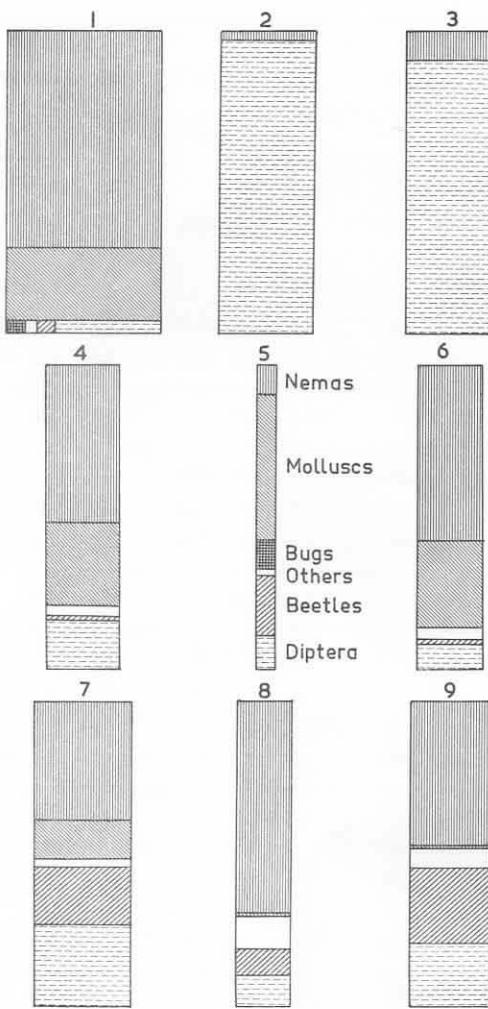


Fig. 3. Analysis by taxonomic groups of herbivore trophic level. Numbers refer to the habitats listed in fig. 2 and Table 1. The total area of each column is proportional to total herbivore metabolism. Different types of shading within a column indicate the proportion of metabolism due to each group as labelled.

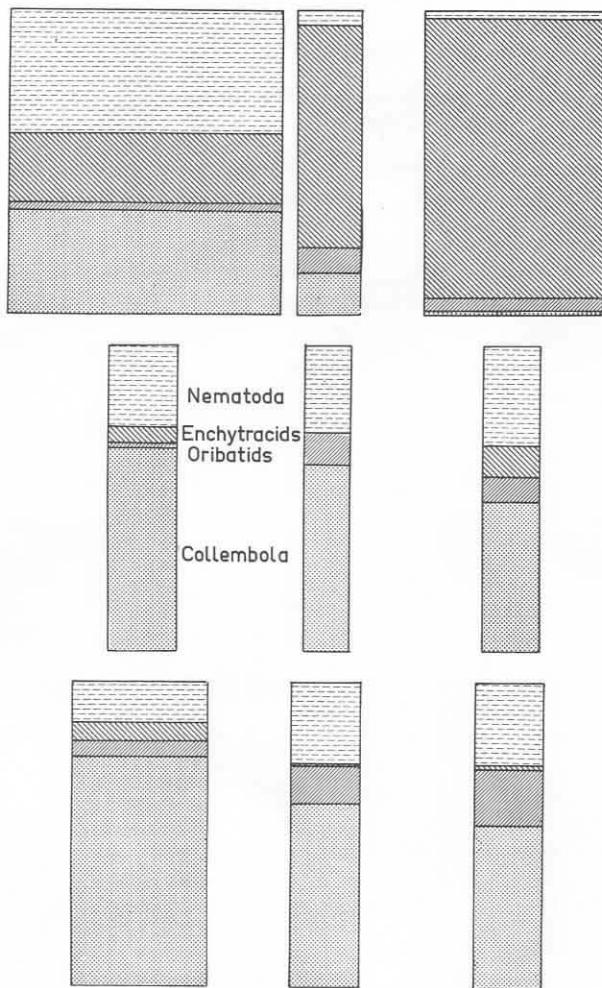


Fig. 4. Small decomposers. For explanation see fig. 3.

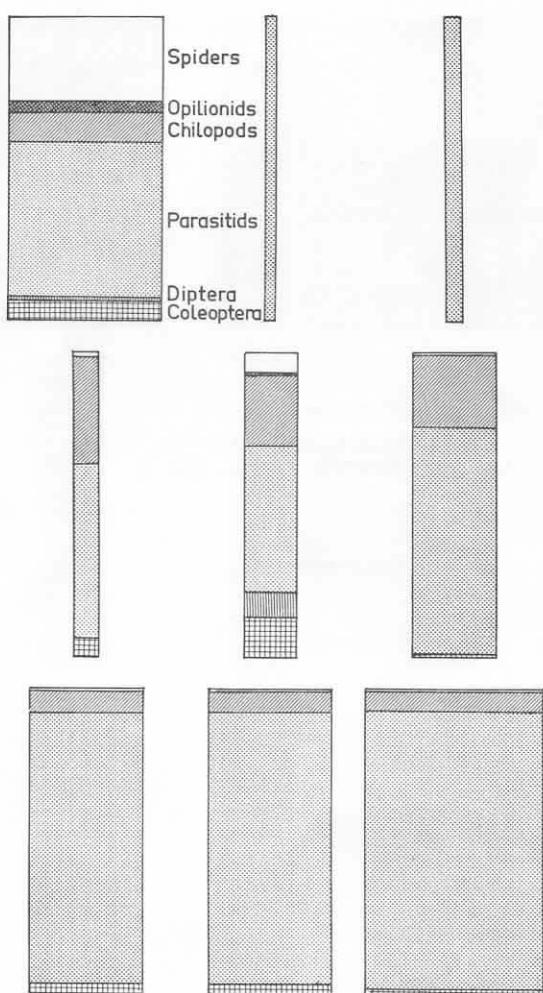


Fig. 5. Predators. For explanation see fig. 3.
Horizontal scale is three times that in figures 3 and 4.

between soils, the proportions of the species within each soil and group varies enormously. It almost seems as though a limited quantity of resources is being shared between the animals in each group and, to take the herbivores (Fig. 3) as an example, the fly larvae and the nematodes each have a limited range of soil types within which they can dominate while amongst the small decomposers (Fig. 4) the enchytraeids, nematodes and collembola can each vary from insignificant to dominant whilst the total metabolic activity remains remarkably constant. This is a phenomenon predicted on theoretical grounds by HAIRSTON, SMITH and SLOBODKIN (1961). Collembola and Oribatids tend to thrive best in fungus-dominated raw humus whilst Nematodes predominate in mineral soils, as discussed by NIELSEN (1949), but the Oribatids take second place to Collembola in most soils owing to their rather low metabolic rates. The diagram for predators (Fig. 5) is the least satisfactory because both census and metabolism results are least accurate and may be positively misleading. I have used my own admittedly limited Parasitid metabolism measurements and have had to assume a 1 : 3 biomass ratio of carnivorous: fungivorous mites when these were not distinguished by the original authors. None the less it seems likely that Parasitids are more important as predators than we had previously thought and that Chilopods are generally very active except in the moorland localities.

A number of authors have commented on the discrepancies in the ratios of metabolic activity to biomass which are shown by members of different trophic groups e.g. GERE (1957), DUNGER (1960). However, as PHILLIPSON (1960) has shown, generalization is difficult and subject to many exceptions in detail. In general the figures in table 1 on a daily basis show small decomposers ranging between 10 % and 20 %, predators 5—20 % while herbivores and large decomposers are mainly below 5 %.

It would certainly be interesting to know the ratio between the total soil metabolism, due to all organisms, and that due to animals alone, but here we run into severe difficulties. Direct measurements on soil microorganisms referable to conditions in nature do not seem to have been made. Gas analysis methods on whole terrestrial ecosystems have been performed by HÜBER (1950) and by GAASTRA (1958) while WALLIS and WILDE (1957) have studied carbon dioxide production by soil and litter *in situ*. Unfortunately their results, perhaps because they were confined to a very short period of time, perhaps due to increased ventilation indicate a respiration rate about 50 times as great as the total rate of supply of organic matter

to the soil. The only remaining method at present of assessing the animals' relative contribution to total activity is by subtraction from the known annual litter fall. In stable communities such as grassland this amounts to the order of 5,000 kcalories per m² and the animals' metabolism is therefore usually between 10 % and 20 % of the total.

It might be thought that figures of this kind indicate that animals are unimportant in soil metabolism as a whole. However we have known since DARWIN's time (1881) that earthworms are important in mechanical mixing and drainage of soil and the catastrophic effects of their elimination by poisons have recently been described by RAW (1962). In addition we have recently been shown by VAN DER DRIFT and WITKAMP (1959, 1960) that the activities of microorganisms can be greatly enhanced by the addition of small arthropods to cultures from which they were absent because, among other things, they promote enormously the germination of fungus spores. Among the mechanisms which seem to be at work in promoting microbial activity the chief seem to be (1) the distribution of spores into sites suitable for germination, (2) the elimination of mycostasis and bacteriostasis and (3) the enrichment of the medium by excreta. In addition the enhancement of microbial colony growth by browsing of senescent colonies — HINSHELWOOD (1951) is probably of considerable importance. Since animals such as mites, Collembola and Nematodes all liberate about 20 % of their own calorific content of energy daily and the arthropods are often wasteful feeders, it can be argued that by these activities and their mobility they act as catalysts of microbial metabolism (MACFADYEN, 1961) and that they influence an energy flow which may be many times that which is channelled through their own bodies.

This is a topic which seems to me of great importance and to be one which could profitably be discussed by the present meeting. It is to be hoped that the microbiologists will give their views on the feasibility of joint studies aimed to measure the magnitude of effects such as those I have mentioned and ultimately to relate them to natural conditions. For my part I have been much impressed by the reproducibility of respiration curves obtained when air dried soil is re-wetted — CHASE and GRAY (1953, 1957); GRIFFITHS and BIRCH (1961); MCKIBBIN and GRAY (1932) and STEVENSON (1956). The introduction of small arthropods in a system of this kind seems a promising compromise between laboratory and field conditions and work on these lines has begun; perhaps our mycologist colleagues will have better suggestions.

I hope that this survey of a limited topic will have met the demands which I outlined at the start by stating one set of view points to the microbiologists in such a way as to show what we are trying to do and at the same time suggesting to my zoological colleagues some methods of generalizing from the rapidly accumulating data which are being produced by their labours.

Summary

Published data are used to derive total annual metabolism estimates for some soil invertebrates in nine contrasting habitats. It is concluded that:

1. Over this range total invertebrate metabolism is closely similar.
2. In mor soils microfaunal activity largely compensates for that of larger species.
3. Herbivore metabolism is rather constant but that of predators varies greatly.
4. Within the main trophic groups the proportion of metabolism due to each taxonomic group varies widely.

The relation between metabolism and other criteria of importance is considered.

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Discussion

G. W. HEATH: Table 1. I found it difficult to understand the production in these two different grasslands. How are these figures obtained?

A. MACFADYEN: The figures were taken from F. B. GOLLEY's paper (*Ecol. Monogr.* **30**, 187—206) and were corrected for English climatic conditions.

G. W. HEATH: It is the essence of agricultural production that it varies from field to field. I do not understand how you can use one figure for production.

A. MACFADYEN: I am speaking generally, comparing distinctly different biotopes.

G. MINDERMAN: I feel sorry that you introduce the Standard Nutritional Unit into biological energy problems, because Megacalories per hectare is very far from the gramcalory and the very small areas we are dealing with up till now. It can only give rise to confusion. As to your diagram of energy flow, by way of the figures you mention for free-organic matter and decomposers I refer to your paper of 1961. From these figures it is possible to calculate the weight of the bacteria and fungi and find approximately 800 g bacteria and fungi oven dry weight per square meter. Referring to the line found in the food consumption of *Glomeris*, *Enchytraeidae*, *Enoicyla* and Nematodes the potential food consumption by the weight of bacteria must be enormous and is in no relation to the amount of available food. Have we to conclude that in soil the bacteria are starving?

A. MACFADYEN: I introduced the N.S.U. in my paper as I thought it is very convenient in relating the energy input and flow with the yield of grazing cattle.

D. PARKINSON: Comparison of the data presented to this symposium by zoologists and microbiologists on oxygen uptake by components of the soil population indicates differences in approach. The relation of O_2 uptake to body weight (by zoologists) is impossible for microorganisms, and thus leads to difficulties in their comparison of data. As far as microorganisms are concerned, although it is not possible to weigh the cells, it is possible to obtain data on the length of mycelium and numbers of bacteria in a unit volume of soil, but we must remember that the presence of a piece of hypha or a bacterial cell does not mean that these entities are active metabolically. Another difference in approach is the relation by microbiologists of O_2 uptake to a unit weight or volume of soil, whereas we see the zoologists relating O_2 uptake to unit area (m^2). To me the relation of activity to area does not seem helpful, and I feel that some uniformity of approach is required by all those studying the activity of the different components of the soil population.

A. MACFADYEN: I agree that the microbiological data make it almost impossible to compare activity with that of animals. The energy flow figures for the former are obtained by difference from total soil metabolism (see p. 14 of my paper) and are not based on counts. Only the "stock" estimates are obtained from the literature (Thornton; Jones and Mollison).

It is hardly possible to argue the justification for an area versus volume basis for our estimates in a short time but briefly we use area because both the incidence of solar radiation and the crop yields obtainable from soil are related to area of land and not to volume of soil.

F. RAW: I should like to know how compensations have been made for differences, in order to obtain the figures in the table. Some of the figures from site 2 and 3 of the *Juncus* moor were obtained from Cragg's data but for several groups they are not available. Bornebusch's figures are underestimates as the technique used was poor. In order to correct this a factor of times 10 or times 100 might have been used. Is it reasonable to make compensations in the light of this?

A. MACFADYEN: The gaps in the figures are probably justified, because such low populations exist.

J. B. CRAGG: I confirm this. The total biomass would not be increased including these small groups.

A. MACFADYEN: Overgaard Nielsen a.o. have pointed out the errors in Bornebusch's figures. It is perhaps encouraging that the figures which I have obtained for earthworms, enchytraeids and oribatids are of the same order as those obtained using the data of Satchell, O'Connor and Berthet.

Miss M. MURPHY: The Protura are not mentioned in this paper. Is this because they do not occur in the soil habitats studied or is it because they are one of the groups the author chose to omit?

A. MACFADYEN: They were not found in significant numbers in the studies reviewed in my paper.

J. B. CRAGG: Can miss Murphy give an idea of the biomass of Protura.

Miss M. MURPHY: Not any, but it is very low.

F. RAW: Protura in some grasslands have relatively a high biomass.

J. B. CRAGG: All of us turned to Bornebusch's figures and did juggle with them. I suggest that for more accurate calculations it would be usefull if our Danish colleagues would work on Bornebusch's sites again.